TWO SPECIES OF *SACCOGLOSSUS* (ENTEROPNEUSTA) FROM SOUTH AUSTRALIA

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A new species of the Enteropneusta, *Saccoglossus aulakoeis* is described. It possesses a deep, dorsal, longitudinal groove on its proboscis. It is compared with three previously described members of the genus which have similar grooves. One of these species, *Saccoglossus otagoensis* (Benham) has been found in the same vicinity. This is a new record for Australia. The two species however, occupy different habitats, *S. aulakoeis* being found in coarse sand and shellgrit in amongst the roots of *Zostera* while *S. otagoensis*, in this locality, has been found only under stones at or below the level of low water spring tides.

During an investigation to determine the distribution of *Saccoglossus apantesis* (Thomas, 1956) in South Australia, two other members of the genus have been found. One of these is a new species and the other a new record for Australia.

Material of both species was fixed in Bouin's-in-seawater and sectioned at 10 μ. Sections were stained either with Ehrlich's haematoxylin and eosin or with Mallory's triple stain. The latter was very effective for showing the basement membrane and the skeletal parts derived from it. Proboscis skeletons were extracted by maceration of unfixed material in 4% borax for several days. After careful cleaning by brushing, they were stained in aniline blue and mounted in cedarwood oil.

Saccoglossus aulakoeis n.sp.

The trivial name is descriptive of the deep, median groove on the dorsal side of the proboscis (αυλαξ = a groove or furrow).

Specimens have been found at Port Willunga, South Australia (lat. 35° 16′ 50″ S, long. 138° 27′ 20″ E) in a shallow tidal pool about half an acre (0·2 hectares) in extent about a quarter of a mile (400 m) south of the ruins of the Port Willunga jetty. The pool is covered to a depth of five or six feet (about 1·6 m) at high spring tides and about half its floor is exposed at low spring tides.

Zostera tasmanica G. V. Martens grows sparsely in small patches at about the level of normal spring lows and in amongst the roots of some of these patches, the enteropneust has been found. It is by no means common. The soil over the underlying rock is not more than an inch or two deep and consists of sand and shell grit with little or no mud. The animal has not been found in sand without *Zostera* and many patches of *Zostera* do not contain it. One specimen has been found in amongst the roots of *Cymodocea antarctica* (Labill.) which grows abundantly in slightly deeper water in the pool. The pool is partly protected by a low, rocky elevation (covered at mid-tide) on its seawards side, but it is open to the sea at all states of the tide.

At Brighton, (lat. 35° 02′ S, long. 138° 31′ E), about thirty miles north of Port Willunga, after a heavy storm, some masses of *Zostera* roots were washed

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ashore on a sandy beach. In amongst the roots were found four fragments of enteropneusts similar in size to the Port Willunga specimens. One of these fragments included a portion of a proboscis with a deep dorsal groove. Sectioning of this material has confirmed that it is *S. aulakoeis*.

The species agrees with the diagnosis of the genus *Saccoglossus* Schimkewitsch, 1892 (syn. *Dolichoglossus* Spengel, 1893) in the possession of the following characters; (a) proboscis very long, (b) collar about as long as broad, (c) lateral genital folds present but dorsal gonads absent, (d) gill pores small but distinct, (e) perihaemal spaces present, (f) posterior oesophageal pores present, anterior ones absent.

EXTERNAL FEATURES

S. aulakoeis (Fig. 1) is a species of small to moderate size. Full grown, intact specimens are difficult to obtain but a specimen of reasonable size which has been relaxed by the method recommended by Ledingham and Wells (1942) (isotonic magnesium chloride), had the following dimensions. Proboscis 16 mm; collar 2·5 mm; branchial region 5 mm; oesophageal region 2 mm; hepatic region 13 mm; intestinal region 24 mm; genital region (which overlaps from the branchial to the hepatic region) 10 mm. The gonads were not fully mature.

The proboscis is orange-red and its base, usually hidden by the collar, slightly darker. On this the preoral ciliary organ (Fig. 1) shows up as a U-shaped yellow line. The anterior three-fifths of the collar is similar in shade to the proboscis. The remaining two-fifths bears two broad, slightly elevated bands, paler and yellower and separated by a narrow groove, the posterior wall of which shows up as a still paler band. This latter band corresponds to zone four in the histological divisions of the collar epidermis (Fig. 6).

Dorsally and laterally, the branchial region is slightly browner than the proboscis and is beset with irregular flecks of yellow-orange. These are groups of gland cells (epidermal glandular eminences, Figs. 1, 7, 8 and 10). The ventral musculature of this region is again similar in shade to the proboscis but with narrow and slightly paler transverse striations (Fig. 1). The oesophageal region is similar in colour to the dorsal branchial region but the flecking, dorsally and laterally, is denser. In the hepatic region, the body wall is somewhat translucent and the surface flecks on the epidermis are smaller and sparser. In living specimens, the deep brown colour of the lateral saccules of the liver region of the alimentary canal show through clearly. The intestinal region, too, is translucent and the sandy gut contents show through. The flecks on the epidermis are still evident but are more widely spaced and are smaller than they are on the hepatic region.

In preserved specimens, the proboscis tapers slightly throughout its length but in living and fully relaxed material, it has the form of a very elongate pear, being appreciably thicker at its base. It has a deep mid-dorsal groove which, at its deepest, is a third to a half of the diameter of the organ and it extends almost to the anterior extremity (Figs. 1 and 4). Posteriorly, in the vicinity of the proboscis complex, it is shallower so that on the basal face of the proboscis, its depth is about one-fifth of the diameter. The preoral ciliary organ has a pattern similar to that in other members of the genus in which it has been described (Brambell and Cole, 1939b; Brambell and Goodhart, 1941; Thomas, 1956). It is U-shaped and lies on the base of the proboscis closer to the stalk than to the outer border of the base. The dorsal tips of its arms, however, are deflected inwards and herein it differs slightly from the organ as it is pictured by Brambell and Cole (1939b) in *S. ruber* (syn. *S. cambrensis* Burdon-Jones and Patil, 1960) in which the arms are

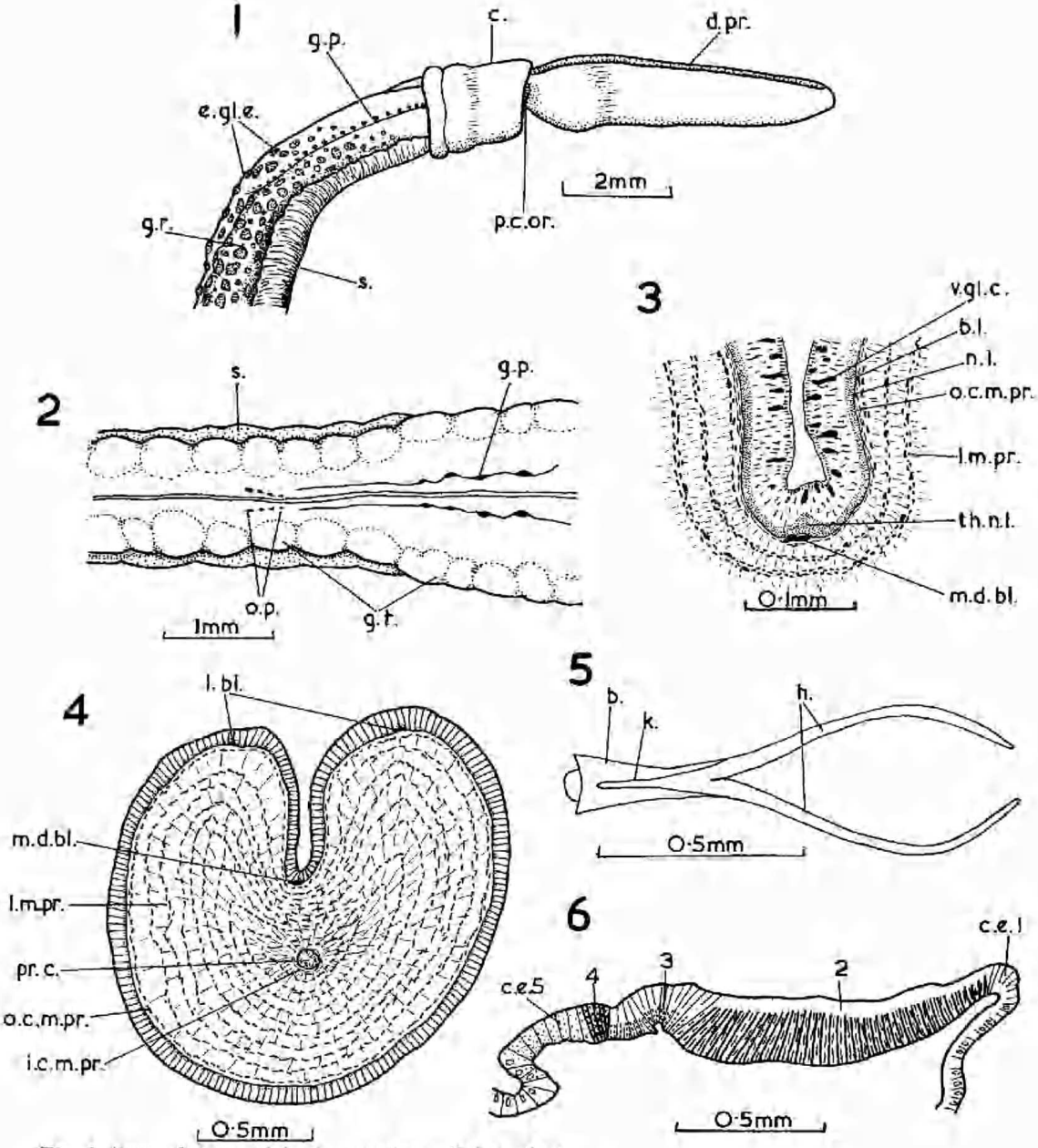

Fig. 1. *Saccoglossus aulakoeis*, anterior end, lateral view.
Fig. 2. Oesophageal region, dorsal view.
Fig. 3. Transverse section, dorsal proboscis groove.
Fig. 4. Transverse section, proboscis.
Fig. 5. Proboscis skeleton, ventral view.
Fig. 6. Zones of collar epidermis. b., body of proboscis skeleton; b.l., basement layer; c., collar; c.e. 1 to 5, zones of collar epidermis numbered from anterior end; d.pr., dorsal groove of proboscis; e.gl.e., epidermal glandular eminence; g.p., gill pore; g.r., genital ridge; h., horn of proboscis skeleton; i.c.m.pr., inner circular muscle layer of proboscis; k., keel; l.bl., lateral blood vessel; l.m.pr., longitudinal muscles of proboscis; m.d.bl., mid-dorsal blood vessel; n.l., nerve layer, o.c.m.pr., outer circular muscle layer of proboscis; o.p., oesophageal pore; p.c.or., preoral ciliary organ; pr.,proboscis; pr.c., proboscis coelom; pr. sk., proboscis skeleton; s., sole, formed by ventral longitudinal muscles; th.n.l., dorsal thickening of nerve layer; v.gl.c., vacuole of epidermal gland cell.

straighter. There is a single, slit-like proboscis pore on the stalk, close to its junction with the collar and slightly to the left of the mid-line.

The collar is longer than its diameter in the proportion of about 1·0 to 0·77. It is also longer dorsally than it is ventrally in the proportion of about 1·0 to 0·85. This is due partly to a slight retraction of the ventral part of the anterior flange under the mouth and partly to the dorsal part of the posterior flange extending farther over the branchial region than does the ventral part (Fig. 1). The posterior two-fifths, approximately, of the collar bears two broad, slightly elevated bands of about equal width and separated by the narrow groove already mentioned.

Anteriorly, the branchial region is somewhat quadrangular in transverse section as most of the main musculature is ventral in position. The ventral surface of the body thus forms a broad sole on which the animal creeps (Fig. 1). Farther back in the branchial region, the sole has a shallow median ventral groove (Figs. 7 and 8).

There are from twelve to twenty-five pairs of small gill pores set in shallow dorso-lateral depressions. The anterior two or three pairs are covered by the posterior flange of the collar. The last five or six diminish in size and get successively closer to the mid-dorsal line (Fig. 2). In small (immature) specimens the first gonads are seen about half-way along the branchial region but in fully mature specimens, they begin closely behind the collar. Depending on the maturity of the specimen, the gonads form more or less conspicuous genital ridges (Fig. 7). In immature specimens (Fig. 8) the ridges are relatively inconspicuous. These extend to the beginning of the hepatic region in mature specimens and end rather abruptly. In immature specimens they do not extend as far back. In the branchial region, the gonads are rather lateral in position but behind the gill pores they become more dorso-lateral (Fig. 2).

About 1 mm behind the last gill pore lie the oesophageal pores (Fig. 2). These are arranged in two rows one on each side of the mid-dorsal line. The pores number from two to seven or eight pairs but the more anterior ones are not patent. The specimen shown in Fig. 10 had two patent (1 and 2) and three rudimentary (3, 4 and 5). The disposition of the rows is variable. Seven specimens were examined in this regard. In three of these the rows were almost parallel to each other and to the mid-dorsal line, in three they were slightly divergent, the more posterior being the farthest apart and in one they diverged at an angle of about 30°. This specimen is shown in Fig. 2. The larger and patent pores are the most posterior. In the anterior oesophageal region the sole (Figs. 7 and 8) is as broad as it is in the posterior branchial region but begins to narrow towards the posterior end of the oesophagus. The hepatic region can be recognized by the more or less regular lateral dilatations of the alimentary canal which can be seen through the somewhat transparent body wall. The sole here narrows further and becomes less in width than the dorsal part of the body though its lateral bulges are still apparent. In the intestinal region the body tapers slightly to the terminal anus and the ventral musculature diminishes in amount so that the sole disappears and the body is rounded in transverse section.

INTERNAL ANATOMY

Proboscis

The glandular and ciliated epidermis of the proboscis extends to the bottom of the dorsal groove and beneath it lies the nerve layer (Fig. 3 and 4). Over most of the proboscis, this is about 12 to 14 μ thick. At the bottom of the proboscis groove there is a marked ridge in the nerve layer so that at this point it is 30 to 32

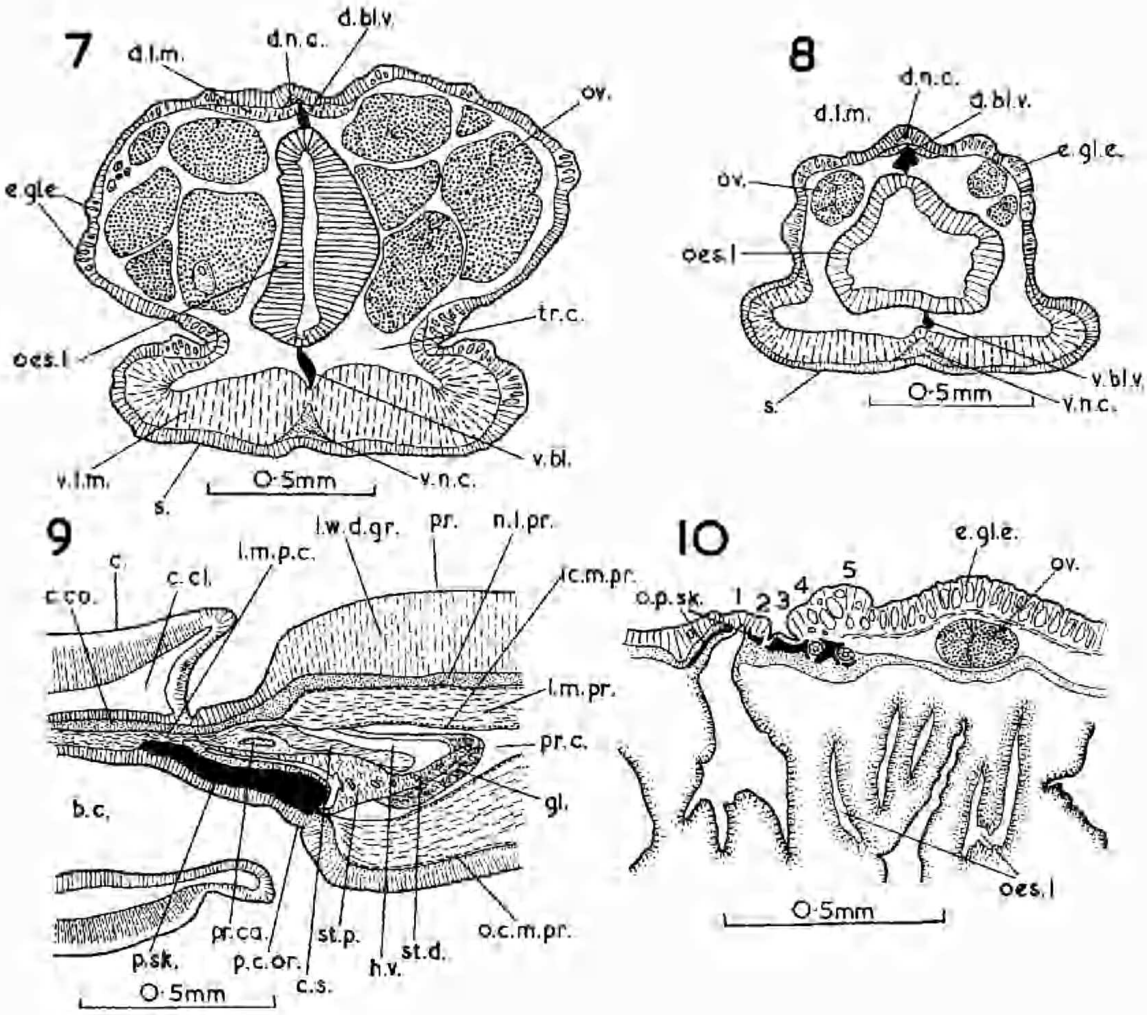

Fig. 7. *Succoglossus aulakoeis*, transverse section of nearly mature female in first region of oesophagus.

Fig. 8. As Fig. 7 but of immature female.

Fig. 9. Longitudinal sagittal section of proboscis complex.

Fig. 10. Longitudinal section showing oesophageal pores. b.c., buccal cavity; c., collar; c.co., collar cord; c.cl., collar coelom; c.s. central sinus (blood sinus); d.bl.v., dorsal blood vessel; d.l.m. dorsal longitudinal muscle; d.n.c. dorsal nerve cord; e.gl.e., epidermal glandular eminence; gl., glomerulus; h.v., heart vesicle (pericardium); i.c.m.pr., inner layer of circular muscles of proboscis; l.m.pr., longitudinal muscles of proboscis; l.m.p.c., longitudinal muscles of perihaemal cavity; l.w.d.gr., vertical section through wall of dorsal groove; m., mouth; n.l.pr., nerve layer of proboscis; o.c.m.pr., outer layer of circular muscles of proboscis; oes. 1, first region of oesophagus; o.p. 1 and 2, first and second oesophageal pores (patent); o.p. 3, 4, and 5, third, fourth and fifth oesophageal pores (rudimentary); o.p.sk., supporting skeleton of oesophageal pores; ov., ovary; pr., proboscis; pr.c., proboscis coelom; pr. ca., proboscis canal (endsac); p.sk., proboscis skeleton; st.d., distal portion of buccal diverticulum; st.p., proximal portion of buccal diverticulum; tr.c., trunk coelom; v.bl., ventral blood vessel; v.l.m., ventral longitudinal muscles; v.n.c., ventral nerve cord.

μ thick (Fig. 3). There is also a general thickening of the nerve layer at the base of the proboscis, particularly under the preoral ciliary organ where it may be three times its normal thickness (Fig. 9) The outer layer of circular muscles immediately under the basement membrane is a half to two-thirds of the thickness of the nerve layer. The longitudinal muscles form nine or ten concentric layers separated by loose connective tissue. These are compressed and barely distinguishable immediately under the dorsal groove (Fig. 4) and they are reduced to five or six in number posteriorly in the vicinity of the proboscis complex (Fig. 9). An inner, thin layer of circular muscles lines the coelomic cavity. The latter extends almost to the tip of the proboscis. Anteriorly it is narrow, being only about one tenth of the diameter of the proboscis, but it expands considerably posteriorly to accommodate the proboscis complex.

Two blood vessels are present immediately outside the outer circular muscle layer on the crests of the ridges formed as the result of the presence of the dorsal proboscis groove (Fig. 4). A small, subneural vessel (median dorsal vessel) has been seen in some specimens in the mid-dorsal line but a median ventral blood vessel has not been observed in specimens so far examined.

The buccal diverticulum (stomochord) (Fig. 9) has a wide, ventral pocket the posterior wall of which is indented by the blunt, anterior tip of the proboscis skeleton. The diverticulum is bent slightly backwards at its tip under the end of the skeleton. The lumen of the pocket is wide and broadly in contact with the main lumen of the buccal diverticulum within the neck of the proboscis but it is not confluent with the buccal cavity. It is occluded at the level of the point of origin of the horns of the proboscis skeleton. Anterior to the ventral pocket, the buccal diverticulum has no continuous lumen, but only a series of unconnected cavities which diminish in size anteriorly. This anterior part of the buccal diverticulum differs from the form usual in the genus in that it is sharply divided into two regions of more or less equal length. The proximal part is thick and conical, while the distal part is very thin being only about one sixth of the diameter of the proximal part at its widest. The distal part is attached anteroventrally and curves dorsally to end near the anterior extremity of the glomerulus. Its cells are much smaller and less vacuolate than those of the proximal part but the separate portions of its lumen are apparent almost to its anterior end.

The glomerulus (Fig. 9) surrounds the distal part of the buccal diverticulum but at the level of the proximal part it is almost entirely lateral and ventral. It ceases posteriorly at the level of the ventral pocket of the buccal diverticulum. The cardiac vesicle (pericardium) and central sinus (Fig. 9) call for no special comment. The dorsal mesentery of the proboscis extends forwards nearly to the level of the constriction of the buccal diverticulum. The ventral mesentery is shorter, extending forwards only to the level of the ventral pocket of the buccal diverticulum. The left coelomic pouch so formed, communicates as is usual in the genus, through the proboscis canal (endsac) with the proboscis pore which is dorsolateral on the left side of the proboscis stalk.

The proboscis skeleton (Figs. 5 and 9) is slender, terminating anteriorly in a rounded tip which partly penetrates the posterior wall of the ventral pocket of the buccal diverticulum. The ventral keel is well formed and posteriorly it bifurcates to become continuous with the horns. These extend about half-way along the collar and embrace about half the circumference of the buccal cavity.

Collar

The five transverse, epidermal zones of the collar distinguished by Spengel (1893) are present (Fig. 6). The first, which overlaps the anterior flange of the collar, contains cells which have large vacuoles distally. This zone merges into the

second. This forms an epithelium, which, at its thickest, is more than three times as thick as the first zone, and occupies nearly three-fifths of the length of the collar. Its cells contain large numbers of small basophil granules in the inner three-quarters of their lengths. The third zone and the fourth and fifth zones combined, form two elevated bands which are readily visible externally. The third and fourth zones are little more than half as thick as the second. The third is histologically similar to the second except in that the basophil granules are concentrated in the inner half to two-thirds of its cells. The fourth zone is by far the narrowest and forms part of the posterior wall of the groove. Its granules are more densely packed and are fairly evenly distributed throughout the length of its cells. In the fifth zone the granules are more sparsely and evenly distributed and towards its posterior end there are peripheral vacuoles which are characteristic of the epithelium of the branchial region with which this zone merges.

The nerve cord of the collar is solid throughout its length. The dorsal mesentery is incomplete and ends anteriorly a little behind the point where the proboscis skeleton divides to form the two horns. The ventral mesentery is more variable in extent. In some specimens it extends as far forwards as the level of the posterior tips of the horns, i.e. about half-way along the collar while in others it is apparent only near the posterior end.

Trunk

The gill pores increase in size over the first two or three and decrease in size over the last four or six. The posterior gill pores are very small and may lack gill pouches. Behind these there may be two or more rudimentary gills. The tongues project farther into the pharynx than do the septa. The gills extend a little more than half-way around the circumference of the pharynx.

In the oesophagus there are three regions. In the first, the epithelium is similar to that of the ventral part of the pharynx but its walls are thicker and have a higher proportion of gland cells. Its lateral walls are irregularly sacculated (Fig. 10). In the second region the walls are much thicker and the lumen correspondingly narrower. At its antero-dorsal end there are deep grooves in the dorsolateral walls into which the oesophageal pores open. Of these, two to five are patent and two to four do not open to the surface but are represented by outpushings of the dorsolateral grooves. There may be corresponding indentations of the epidermis above them. All are supported by skeletal elements which usually fuse to form an almost continuous plate which is perforated in the positions of the patent and the non-patent pores. These elements are, like the other skeletal structures of the animal, thickenings of the basement layer which underlies the nerve layer over the whole of the body. In the third region of the oesophagus the walls are thinner and the lumen wider. Laterally there is an irregular sequence of shallow pouches. This region merges into the hepatic region which differs from it mainly in that the lateral pouches are larger and more regularly arranged. In the intestinal region, the alimentary canal is simple. Its wall is thin and the lumen wide. There are however, two ventral thickenings separated by a narrow, median, longitudinal groove which extend nearly to the posterior end.

COMPARISON WITH OTHER SPECIES

Three other species of *Saccoglossus* have been described as possessing deep dorsal grooves on the proboscis. These are *S. mereschkowskii* (Nic. Wagner) 1885, *S. otagoensis* (Benham) 1899, and *S. sulcatus* (Spengel) 1893. While the first two have been adequately described (van der Horst, 1939), the third was described from three anterior ends only which became dried up so that detailed examination was impossible (Spengel, 1893).

The main differences between these three species and S. *aulakoeis* are listed in Table 1. The relevant data on S. *mereschkowskii*, S. *otagoensis* and S. *sulcatus*, have been taken, in the main, from van der Horst, 1930 and 1939.

S. *aulakoeis* is established on its possession of the following combination of characters.

1. A deep dorsal proboscis groove.
2. The ventral musculature forms a prominent "sole" in the posterior branchial and oesophageal regions.
3. The collar is slightly longer than broad.
4. The fourth epidermal zone of the collar epidermis is very narrow.
5. There are two to five pairs of patent oesophageal pores preceded by two to four rudimentary ones.
6. The longitudinal muscles of the proboscis are arranged in nine or ten concentric layers.
7. Epidermal gland cells extend to the bottom of the proboscis groove.
8. The glomerulus covers the anterior end of the buccal diverticulum.
9. The buccal diverticulum has a very narrow distal portion which is not conspicuously bent and in which the lumen is incomplete.
10. The proboscis skeleton is bluntly rounded anteriorly.
11. There are no cavities in the dorsal nerve cord of the collar.

DISCUSSION

S. *aulakoeis* has been found only in the restricted regions indicated in the introduction. Even here it is not common. It is rare to find as many as two or three specimens in a spadeful of soil. It is interesting however, that frequently specimens varying in size from 1·5 cm to 5·5 cm may be found at the same time. This suggests that the breeding season for the species is an extended one or that there is a considerable variation in growth rate. However, animals with mature or maturing gonads are generally seen in late winter and early spring (Fig. 7), while in the summer months the gonads are invariably small (Fig. 8). Mature specimens do not coil markedly in the post-branchial and oesophageal regions as do those of S. *apantesis* (Thomas, 1956). This is, no doubt, to be associated with the lesser degree of development of the genital ridges.

In all specimens examined, with the exception of those fixed without adequate narcosis, the collar is slightly longer than it is broad. The definition of the genus states that the collar is "about as long as it is broad". The proportion of the length to breadth of 1·0 to 0·77 is considered to fall within the limits of the definition but the extent of the ratio is noteworthy.

Non-patent oesophageal pores have been described for S. *ruber* (syn. S. *cambrensis* Brambell and Cole, 1939) and they also occur in the present species. It will be necessary to determine their presence or absence in several other forms before reasons for their existence can be discussed.

There is a possible association between the dorsal thickening of the nerve layer and the dorsal groove of the proboscis. Both S. *otagoensis* and S. *aulakoeis* have deep dorsal grooves and a thickening of their nerve layers. Similar thickenings of the nerve layers have been described in S. *ruber* and in S. *horsti* (Brambell and Goodhart, 1941) and in these too there is a dorsal groove in the proboscis

though it is not nearly as deep as it is in the first two species named. In *S. apantesis* however, the dorsal groove is only slightly developed and the thickening of the nerve layer is also slight.

While the description of this species was being prepared, some specimens which clearly belonged to the same genus were found under stones on Snapper Point. This lies about half a mile (about 800 m) south of the pool in which *S. aulakoeis* had been found. These specimens were at first thought to be the same species as they also had a deep dorsal groove on the proboscis. Closer examination and later, a study of longitudinal and transverse sections showed that this was not the case but that they were *Saccoglossus otagoensis* (Benham).

Balanoglossus otagoensis, Benham, 1899

Dolichoglossus otagoensis, (Benham) van der Horst, 1930

Saccoglossus otagoensis, (Benham) van der Horst, 1939 (p. 399)

This is the first record of the species outside New Zealand. Three fairly complete specimens and two fragments were found under stones in about one foot of water at low tide on the northern (more sheltered) side of Snapper Point Reef (lat. 35° 17′ S, long. 138° 26′ 30″ E). This is an extensive wave-cut platform of almost horizontally bedded sandy limestone of Pliocene age. It is relatively hard in parts but on its northern border and in some other regions, it is softer and somewhat friable. Thus, along its northern margin, a secondary, narrow reef flat has been formed about two feet below the general level of the main reef. This is covered by about a foot of water at normal spring lows. One specimen was found under a stone in a permanent rock pool about six inches deep on the main reef surface.

It is a crawling rather than a burrowing species, as is *S. aulakoeis* and it agrees closely with the description of *S. otagoensis* as given by Benham (1899), and van der Horst (1930 and 1939). The points of undeniable resemblance are asterisked in Table 1. In regard to the remaining points listed, the collar is rather shorter than it is broad in the proportion of about 1·0 to 0·70. This may be due to contraction in fixation. The specimens from Snapper Point are relatively immature so that the irregularity in the lateral genital bulges is not very apparent. In regard to the presence of gland cells in the proboscis groove, van der Horst (1930) states that they are absent from the base of the groove and his Fig. 2 (p. 137) shows them to be present in the lateral walls. This is the case in the Snapper Point specimens too. However in his diagnosis of the species (1939) he says "Keine Drüsenzellen in der Epidermis in der dorsalen Furche", which implies that they are absent from the groove altogether. This seems to be an oversight as they are present in the walls of the groove (though not at its base) in specimens in the author's possession which were collected at Portobello, New Zealand, which is close to the type locality of the species.

Van der Horst (1930 p. 139 and 1939 p. 661) describes the buccal diverticulum as having two marked flexures in front of the ventral diverticulum. This is figured in his 1930 description (Fig. 4, p. 139). The Snapper Point specimens do not have these marked flexures. It is felt that these may well be fixation artifacts in van der Horst's specimens.

In New Zealand, the species is found in amongst coralline algae at Wellington and amongst the holdfasts of *Macrocystis* at Portobello. This shows it to be a crawling rather than a burrowing species and indeed, Benham in his original account of the species writes of it as crawling on a stem of seaweed.

TABLE 1

Comparison of diagnostic features of *Saccoglossus otagoensis*, *S. mereschkowskii*, *S. sulcatus* and *S. aulakoeis*.

S. mereschkowskii	*S. otagoensis*	*S. sulcatus*	*S. aulakoeis*
External Features			
Collar about as long as broad	Collar about as long as broad	Collar about as long as broad	Collar slightly longer than broad
Genital folds more or less regular appearing in female only	Genital folds in form of irregular bulges in female	—	Genital folds fairly regular in both male and female
—	No epidermal glands in base of dorsal proboscis groove	—	Epidermal glands present in base of dorsal proboscis groove
Longitudinal muscle in 7 to 10 concentric rings	*Longitudinal muscles in 3 or 4 concentric rings		Longitudinal muscles in 9 or 10 concentric rings
Proboscis			
—	*Cavity of buccal diverticulum may open into mouth cavity	—	Cavity of buccal diverticulum does not open into mouth cavity
Lumen of buccal diverticulum continuous	*Lumen of buccal diverticulum continuous	—	Lumen of buccal diverticulum not continuous anterior to ventral pocket
Buccal diverticulum relatively straight	Buccal diverticulum with marked ventral then anterior flexures; narrow anteriorly	—	Buccal diverticulum very narrow anteriorly but without marked flexures
Glomerulus covers nearly all of buccal diverticulum	*Two halves of the glomerulus not united in front of buccal diverticulum	—	Glomerulus extends anteriorly beyond tip of buccal diverticulum
Anterior tip of proboscis skeleton with long, sharp point	*Anterior tip of proboscis skeleton with long, sharp point	—	Anterior tip of proboscis skeleton bluntly rounded

S. mereschkowskii	*S. otagoensis*	*S. sulcatus*	*S. aulakoeis*
Collar			
—	*Horns of proboscis skeleton horizontal and reach hinder end of collar	—	Horns of proboscis skeleton extend about half-way along collar and embrace about half mouth cavity
Epidermis very thick (0.05 mm)	*Epidermis of normal thickness	—	Epidermis of normal thickness
—	*Three epidermal zones	—	Five epidermal zones
Dorsal and ventral mesenteries present but incomplete	*Dorsal and ventral mesenteries absent	—	Dorsal and ventral mesenteries present but incomplete
Cavities in dorsal nerve cord	*Cavities in dorsal nerve cord	—	No cavities in dorsal nerve cord
Trunk			
—	*Ventral longitudinal muscles of trunk do not form lateral ridges	—	Ventral longitudinal muscles form conspicuous lateral ridges
About 50 pairs of gills	*10 to 15 pairs of gills	10 to 11 pairs of gills	12 to 25 pairs of gills
Oesophagus with 3 sections	Oesophagus with 6 sections	—	Oesophagus with 3 sections
About 7 pairs of oesophageal pores	*One pair of oesophageal pores	—	2 to 5 pairs of patent oesophageal pores and 2 to 4 pairs of rudimentary pores
	*Seldom more than 3 ripe ova in one ovary	—	6 or more ripe ova in one ovary
Location			
Northern Russia to the Sea of Okhotsk	New Zealand and St. Vincent Gulf, South Australia	Japan	St. Vincent Gulf, South Aust.

* Indicates points of similarity between South Australian and New Zealand specimens.

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